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VERTICAL STRATIFICATION OF HILLTOPPING BEHAVIOR IN SWALLOWTAIL BUTTERFLIES (PAPILIONIDAE)

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ABSTRACT. A study of hilltopping behavior in Papilioninae on a forested hilltop in Tennessee has revealed a vertical zone for *Papilio glaucus* L. separate from other Papilioninae. These findings suggest that perception of "hilltop" differs among species. Separate hilltop vertical zones for species occupying the same horizontal habitat increase the species-packing capacity of the habitat and may increase the likelihood of successful mate location by reducing the interspecific encounter rate.

Additional key words: *Papilio glaucus*, mate locating behavior, patrolling, Tennessee.

Hilltopping behavior is common in butterflies and is characteristic of many swallowtails. A number of excellent studies and reviews detail this mate locating behavior (Shields 1967; Scott 1968, 1975, 1982; Guppy 1969; Lederhouse 1982; Alcock 1985). Studies of hilltopping Lepidoptera in the United States have been predominantly in western areas with open hilltops. In this study I examined the behavior of Papilioninae on a forested hilltop in the southeastern United States.

STUDY AREA

The hill studied is located in southeast Giles County, Tennessee, an area of rough topography with high winding ridges, hills, and deep meandering valleys of the Highland Rim. The underlying rocks are sedimentary, primarily limestone. The hilltop is 262 m in elevation, entirely tree covered, relatively flat, and oval shaped. The surrounding valley is 200–213 m elevation with hill slopes ranging in grade from 30 to 45% and slightly steeper to the west. The canopy on the hilltop is 15–25 m high, with crowns beginning at approximately 10 m. Canopy height is greater on the eastern slope than on the western slope. Trees 6–12 m in height are present in the understory. The predominant tree species are hickory (*Carya ovata*) (Juglandaceae) and hackberry (*Celtis occidentalis*) (Ulmaceae). Other deciduous tree species are scattered throughout, but no evergreen trees are present.

Tree density allowed 20–50% of the forested ground area to receive sunlight even during seasonally maximal crown development, depending on the time of day. Ground cover consisted primarily of vines and small bushes with some native grasses and weeds, but generally was devoid of flowers. Although this hill is one of the highest within a 2 km radius, at least 20 other hills over 245 m in elevation occur in the area.

METHODS

The oval, relatively flat summit was divided into four quadrants with the long-axis of the oval running N/S and the short axis running E/W. The study site was defined as the area extending from the center point of the hill to 2 m descent, resulting in an oval area 69 m long and 48 m wide. Each quadrant of the study area was divided into vertical zones defined by height above ground as low (<3 m), intermediate (3–6 m), and high (>6 m).

Butterfly surveys of five minutes duration were conducted between 1000 h and 1500 h (CDST) in all four quadrants in counterclockwise sequence, rotating the initial quadrant and providing rest intervals of 20–40 min after all four quadrants were observed. Papilioninae in each quadrant were counted and recorded as to vertical zone location. A single butterfly was counted for each vertical zone entered in each quadrant, but only once for each zone while in that quadrant. Thus, a single species flying from low to high vertical zone in the same quadrant was counted in all three zones. In addition to the author, one to three observers counted and followed each butterfly in each quadrant. The primary purpose of the observers was to insure that a butterfly was not missed or counted twice, particularly in the canopy area. Dull or camouflage clothing was worn by all observers and no specimens were collected during observation periods. Non-Papilioninae species interacting with Papilioninae species were observed and their behaviors recorded, but quantitative data were collected only for Papilioninae.

Observations were made between 3 April and 27 August 1989 and quantitative data were collected between 8 July and 27 August 1989. Wind direction and velocity at the summit ground level were measured by WinDial (Edmund Scientific, Barrington, New Jersey 08007). Relative wind velocity was estimated at treetop level by visually assessing movement of the tree crowns. Ambient air temperature in the shade at the hilltop was recorded with an Ultimeter (Edmund Scientific), and general weather conditions were noted.

RESULTS

Species of Papilioninae (Papilionidae) visiting the hilltop included *Eurytides marcellus* Cramer, *Papilio cresphontes* Cramer, *Papilio glaucus* L., *Papilio troilus* L., *Battus philenor* L., and *Papilio polyxenes asterius* Stoll. Collectively, *P. troilus*, *P. cresphontes*, *B. philenor*, and *E. marcellus* were seen 288 times, 286 of which were in the low vertical zone (Table 1). The intermediate and high vertical zones were entered only rarely by these species. *Papilio troilus* and *B. philenor* were each present only once, in the intermediate vertical zone. *Papilio cresphontes*

TABLE 1. Summary of hilltop observations of Papilioninae according to vertical zone location.

Species	Vertical zone		
	High	Intermediate	Low
P. glaucus	319	13	8
P. troilus	0	1	128
B. philenor	1	1	83
P. cresphontes	0	3	63
E. marcellus	0	0	12

moved from low to intermediate zone three times on leaving the hilltop and once, when pursued by another butterfly, *B. philenor* moved from the low to the intermediate vertical zone and briefly into the high vertical zone before returning to the low vertical zone after the pursuit ended. The low number of observations of *E. marcellus* probably results from the study taking place late in this species' flight season. *Papilio polyxenes* was encountered so infrequently as to preclude its assignment to a characteristic vertical zone.

Typical patrolling behavior (Scott 1974) was exhibited by all Papilioninae in the low vertical zone, although *B. philenor* often perched on vines and small bushes. *Papilio troilus* occasionally exhibited similar perching behavior. *Papilio cresphontes* tended to fly higher above the ground in the low vertical zone than the other species, but remained in the low vertical zone on the summit. Interaction among all species in the low vertical zone was common. The intermediate vertical zone was not patrolled by Papilioninae.

There were 320 observations of *P. glaucus,* of which 319 were in the high vertical zone (Table 1). *P. glaucus* entered the intermediate vertical zone from the high vertical zone only 13 times, continuing into the low vertical zone 7 times. All 7 episodes of entrance into the low vertical zone occurred when *P. glaucus* was being pursued by another *P. glaucus* or by another species. At the end of each such encounter, the *P. glaucus* returned to the high vertical zone without interaction with another butterfly. *Papilio glaucus* predominated in the high vertical zone and other Papilioninae predominated in the low vertical zone. This difference is highly significant (Chi square, *P. glaucus* versus non-*glaucus* and high zone versus low zone, is 578.7: $P < .0005$).

Other species present on the hilltop that interacted with Papilioninae in all three vertical zones included *Asterocampa celtis* Bvd. & Lec. (Apaturidae) and *Limenitis arthemis astyanax* Fabr. (Nymphalidae). These two perching species were present in all three vertical zones although *L. arthemis astyanax* was observed predominantly in the intermediate and high vertical zones. Perching male *A. celtis* appeared

to be as frequent in surrounding nonhilltop areas as in the study area, whereas perching male *L. arthemis astyanax* were uncommon off the hilltop. Although *P. glaucus* interacted with these two species, there was no pursuit interaction between *P. glaucus* and other Papilioninae on the hilltop.

There were no changes in vertical zone location for any of the species that could be correlated with direction or velocity of wind, intensity of sunlight, or time of day. Wind direction was almost always from the west, northwest, or southwest. At high wind velocities, *P. glaucus* was more likely to be observed in the leeward side of the study area. With calm or light wind, *P. glaucus* was equally represented in all four quadrants in the high vertical zone. In the low vertical zone, wind velocity never reached more than 8 kmp because of the windbreak effect of the trees. Species in the low vertical zone were present in all hilltop quadrants equally.

DISCUSSION

This study clearly demonstrates a three-dimensional aspect to hilltopping behavior in a forested area, a result not previously reported. Previous studies examining hilltopping behavior have dealt primarily with treeless or predominantly treeless hilltops, most often in the western United States (Shields 1967, Lederhouse 1982, Scott 1982, Alcock 1985). Guppy (1969) reported that he had never seen butterflies on a particular densely wooded hilltop area, but that a sparsely wooded summit was frequented by butterflies. The forested hilltop in this study is probably representative of many such areas in the southeastern United States.

Scott (1968, 1982) demonstrated that hilltopping behavior is a mate-locating behavior characteristic of low density species. Shields (1967) provided evidence that "hilltopping" in butterflies is a phenomenon in which males and virgin (or multiple-mating) females instinctively seek a topographic summit to mate.

In the present study, there is an apparent species-specific difference in perception of what constitutes the "hilltop." *Papilio glaucus* seeks a higher vertical zone than other Papilioninae, flying mostly at treetop level on forested summits. Other Papilioninae prefer ground level at the summit (similar to any open hilltop area). Possible explanations for *P. glaucus*'s preference for the high vertical zone in this forested area include the following: greater requirement for sunlight, presence of attractants in the tree crown region, safety from predators, more efficient use of air currents and thermal uplifts for gliding movements, and reduced interaction with non-*glaucus* species.

Weather conditions such as temperature and solar radiation levels have been shown to influence the male density of hilltopping species,

but not their behavior (Wickman 1988). Similarly, no vertical zone changes occurred with any species in this study despite changing sunlight exposure (sunny, partly cloudy, or cloudy). Furthermore, *P. glaucus* was observed in the high vertical zone in early spring prior to the appearance of treetop foliage. Thus, sunlight intensity is an unlikely cause for the vertical zone behavior.

There was no evidence of any attractant in the canopy, and *P. glaucus* exhibited typical patrolling behavior. Although *P. glaucus* did occasionally alight in the canopy, there was no predilection for any particular tree species and patrolling behavior soon resumed.

Potentially, *P. glaucus* would have greater ability to descend rapidly and maneuver away from predators by patrolling in the high vertical zone, but this seems an unlikely reason for its persistence in the high zone location. Furthermore, there may be greater numbers of predators in the canopy than in the low vertical zone.

Shields (1967) found that hilltopping species confine their activities to the leeward side of the summit during windy periods. My observations of *P. glaucus* reported here extend these findings to the canopy level on forested summits. Soaring and gliding movement of *P. glaucus* is reminiscent of avian species (Brown 1963, Dorst 1974), which take advantage of wind currents and thermal uplifts for energy conservation during flight. Reduced energy expenditure may be even more important to patrolling male butterflies and this could be a factor in *P. glaucus*'s preference for the high vertical zone. But this reasoning should apply to all patrolling species and thus does not explain why *P. glaucus* is the only papilionid found in the high vertical zone.

Reduced interaction with non-*glaucus* species is probably the most important factor responsible for high vertical zone behavior of *P. glaucus*. Scott (1974) discussed energy conservation and the importance of separate mating sites to reduce interference between species. He suggested that if closely related species already mate in one site, then interference between those species may select for mating in another site. Exploiting an area unoccupied by other Papilioninae would result not only in energy conservation for the patrolling male, but would increase the likelihood that any encounter would result in locating a conspecific female. Separate vertical zones for species occupying the same horizontal habitat increase the species-packing capacity of the habitat and reduce the chances of interspecific interaction, thus increasing the likelihood of successful encounters among potential mates.

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